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Review

Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control

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Agricultural intensification has resulted in a simplification of agricultural landscapes by the expansion of agricultural land, enlargement of field size and removal of non-crop habitat. These changes are considered to be an important cause of the rapid decline in farmland biodiversity, with the remaining biodiversity concentrated in field edges and non-crop habitats. The simplification of landscape composition and the decline of biodiversity may affect the functioning of natural pest control because non-crop habitats provide requisites for a broad spectrum of natural enemies, and the exchange of natural enemies between crop and non-crop habitats is likely to be diminished in landscapes dominated by arable cropland. In this review, we test the hypothesis that natural pest control is enhanced in complex patchy landscapes with a high proportion of non-crop habitats as compared to simple large-scale landscapes with little associated non-crop habitat. In 74% and 45% of the studies reviewed, respectively, natural enemy populations were higher and pest pressure lower in complex landscapes versus simple landscapes. Landscape-driven pest suppression may result in lower crop injury, although this has rarely been documented. Enhanced natural enemy activity was associated with herbaceous habitats in 80% of the cases (e.g. fallows, field margins), and somewhat less often with wooded habitats (71%) and landscape patchiness (70%). The similar contributions of these landscape factors suggest that all are equally important in enhancing natural enemy populations. We conclude that diversified landscapes hold most potential for the conservation of biodiversity and sustaining the pest control function.

Keywords: agroecosystems; biological control; ecosystem functioning; landscape diversity; parasitoid; predator

1. INTRODUCTION

The intensification of agricultural production systems has resulted in a dramatic change in agricultural landscapes in Western Europe and North America (Robinson & Sutherland 2002). The expansion, up-scaling of field sizes and clearing of agricultural land have resulted in a simplification of agricultural landscapes containing only small fragments of natural habitats. There is accumulating evidence that these changes in land use, in combination with high agrochemical input in crop fields, are the primary causes for the rapid decrease of biodiversity in many of these landscapes (Robinson & Sutherland 2002; Benton *et al*. 2003).

Concerns have arisen about the deterioration of ecosystem functions in simplified landscapes as a result of the loss of biodiversity. An important ecosystem function that has been associated with biodiversity is natural pest control (Ives *et al*. 2000; Wilby & Thomas 2002; Gurr *et al*. 2003). The suppression of pest populations in crops by natural enemies provides environmental and economic benefits because it may reduce yield loss without the negative environmental consequences that result from chemical pesticide use (Naylor & Ehrlich 1997; Östman *et al*. 2003). However, the role of biodiversity in maintaining natural pest control is controversial and needs more scientific support to be accepted as a basic principle by farmers. Rodríguez & Hawkins (2000) and Finke & Denno (2004) showed that a simplified natural enemy community provides control of pest populations that is equal to or better than a complex of natural enemies. These findings are in line with observations from biological control programs showing that effective control can in most cases be achieved by the introduction of one or few natural enemies (Myers *et al*. 1989). In contrast, there is also empirical evidence that diverse communities of natural enemies are more effective in regulating herbivore populations than poor communities (Losey & Denno 1998; Cardinale *et al*. 2003; Schmidt *et al*. 2003; Snyder & Ives 2003). At this point, general conclusions on the relation between biodiversity and the natural pest control function are uncertain.

Landscape composition affects the diversity and abundance of the natural enemy complex because

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different habitat types may favour different natural enemy species. A diversified agricultural landscape mosaic may therefore sustain a broad diversity of natural enemies. Non-crop habitats are often favourable habitats for natural enemies and act as source habitats from which the less favourable agricultural fields are invaded. Only when natural enemies have a year-round preference for non-crop habitats may they act as sinks relative to crop habitats. The extent to which a habitat functions as source or sink depends on its quality and size in relation to that of the surrounding habitats (Dunning *et al.* 1992). The benefit to the farmer of a diversified landscape in this context is increased when (i) the natural enemy populations are higher and more diverse, (ii) natural enemies substantially colonize arable fields, (iii) they significantly reduce pest densities, (iv) thereby reducing damage levels and (v) increasing yield or quality and (vi) benefits outweigh costs. Achieving economic benefit by natural pest control thus depends on a set of critical steps. In addition, non-crop habitats may not only act as reservoirs for natural enemies, but also for pest species that invade crops (van Emden 1965). Benefits of natural pest control are therefore not self-evident, but depend on many factors and can easily be disrupted.

There are a limited, but growing number of studies that focus on how landscape context affects interactions between natural enemies, herbivores and primary production, thereby integrating concepts of landscape ecology and conservation biological control. Multi-functional landscapes, which promote biodiversity and provide favourable conditions for agriculture based on ecological principles, may contribute to the development of productive yet sustainable agricultural systems. An overview of our current knowledge is needed to assess the potential synergy between biodiversity conservation and ecosystem services relevant for sustainable agriculture. There are several recent reviews that address conservation issues in agricultural landscapes. However, Landis *et al.* (2000) review all aspects of habitat management but give no systematic review of landscape effects and the value of non-crop habitat in agricultural landscapes for pest control. The effects of agri-environmental schemes, set-aside and organic agriculture on biodiversity are reviewed by Kleijn & Sutherland (2003), Van Buskirk & Willi (2004) and Bengtsson *et al.* (2005), respectively, but do not discuss the role of landscape composition and biocontrol. A review of the relatively few and scattered publications focusing on the role of landscape composition for biodiversity (with emphasis on natural enemies) and its relation to ecosystem functioning (biocontrol in crop fields) may give more insight regarding general patterns and research needs.

This review focuses on how landscape composition affects biodiversity and natural pest control in agroecosystems. Although the review focuses on the temperate zone (North America and Europe), the mechanisms underlying biodiversity–pest control relationships are general and are also relevant for other regions. First, we show that non-crop habitats play an essential role in the conservation of biodiversity in agricultural landscapes and highlight the ecological significance of these habitats for natural enemies that have the potential to suppress pest populations. Second, we provide an overview of publications that have quantified the activity of natural enemies and pest pressure in landscapes with variable proportions of non-crop habitats. In a coarse-scale analysis we test the hypothesis that landscapes that hold most biodiversity also exhibit the best natural pest control function. In a fine-scale analysis, we identify landscape features that are associated with successful natural pest control. We conclude with a discussion in which we summarize the current status of this research field and provide suggestions for future research.

2. ECOLOGICAL SIGNIFICANCE OF CROP AND NON-CROP HABITATS FOR BIODIVERSITY CONSERVATION

Agroecosystems hold a large proportion of the world's biodiversity (Pimentel *et al.* 1992). However, there is increasing evidence that the expansion of agricultural intensification has contributed to a rapid decline of biodiversity in agroecosystems (Barr *et al.* 1993; Chamberlain *et al.* 2000; Robinson & Sutherland 2002; Benton *et al.* 2003). For instance, Wilcove *et al.* (1998) estimated that 38% of the endangered species in the United States are negatively affected by agricultural practices. Changes in landscape composition and intensive management practices are considered to be the main factors causing this decline.

In intensively used agricultural areas, arable fields are the dominant landscape element and although different crops are perceived differently by species (Honěk 1982; Ryszkowski *et al.* 1993; Duelli *et al.* 1999), all field cropping systems are ephemeral habitats that are subject to frequent and intensive disturbances (Landis & Marino 1999). Consequently, crop habitats are hostile environments for many species and biodiversity is concentrated in more stable non-crop habitats and field edges (Barr *et al.* 1993; Kleijn *et al.* 2001; Meek *et al.* 2002). This is also true for many insect species and, in particular, natural enemies of insect herbivores (Duelli *et al.* 1999; Klein *et al.* 2002; Duelli & Obrist 2003; Kruess 2003; Schmidt & Tscharntke 2005*b*). Many species occurring in intensively managed cropping systems must be able to move between non-crop habitats and fields at critical times, such as harvest, and colonize fields at the start of the growing season in order to be effective control agents (Wissinger 1997).

Non-crop habitats such as field margins, fallows (set-aside land), hedgerows and wood lots are relatively undisturbed and temporally permanent areas that hold a substantial proportion of the biodiversity in agricultural landscapes. These habitats have been reported to act as biodiversity reservoirs for plants, insects, birds and mammals (Johnson & Beck 1988; Barr *et al.* 1993; Hinsley & Bellamy 2000; Perfecto & Vandermeer 2002; Duelli & Obrist 2003; Van Buskirk & Willi 2004). As a consequence, heterogeneous landscapes composed of arable fields intermingled with non-crop habitat support a higher biodiversity than simplified, coarse-grained landscapes composed of mainly arable fields (Banaszak 1992; Tscharntke *et al.* 1998; Weibull *et al.* 2000; Söderström *et al.* 2001; Steffan-Dewenter 2002, 2003; Kruess 2003; Weibull & Östman 2003; Weibull *et al.* 2003; Purtauf *et al.* 2005*a*,*b*; Schmidt *et al.* 2005).

3. ECOLOGICAL SIGNIFICANCE OF NON-CROP HABITATS FOR PESTS AND NATURAL ENEMIES

Non-crop habitats in rural landscapes often comprise woody (e.g. forests and hedgerows) and herbaceous habitats (e.g. field margins, road verges, fallows and meadows). A number of agricultural pest species are associated with these habitats, such as aphids, herbivorous flies and beetles (e.g. Langer 2001; Denys & Tscharntke 2002). Non-crop habitats also support a diversity of natural enemies, including carabid beetles (e.g. Varchola & Dunn 2001), staphylinids (e.g. Maudsley *et al.* 2002), spiders (e.g. Schmidt & Tscharntke 2005*b*), coccinellids (e.g. Honěk 1989), syrphids (e.g. Cowgill *et al.* 1993), chrysopids (e.g. Sengonca *et al.* 2002), predatory mites (Rieux *et al.* 1999), parasitoids (e.g. Kruess & Tscharntke 1994), predacious Heteroptera (e.g. Nicholls *et al.* 2001) and insectivorous birds (references cited in Dix *et al.* 1995).

Vegetation associated with woody and herbaceous habitats, such as *Vaccinium* spp., *Cornus* spp., *Ilex* spp. (Maier 1981), *Fraxinus* spp. (Rieux *et al.* 1999), *Crataegus* spp. (van Emden 1965) and *Urtica* spp. (Perrin 1975) may support alternative hosts and prey for parasitoids and predators. Landis & Menalled (1998) report that over 60% of the alternative hosts of generalist parasitoids that control lepidopteran pests in corn, soybean, wheat and alfalfa feed on trees and shrubs. Presence of alternative hosts and prey may increase parasitoid and predator populations, resulting in improved pest control (Maier 1981; Settle *et al.* 1996; Bianchi & van der Werf 2004; Östman 2004).

Woody and herbaceous vegetation may also act as sources of pollen and nectar, which are essential prerequisites for many insects (Bugg *et al.* 1998). For example, the longevity and fecundity of parasitoids are substantially increased when nectar sources are available (Baggen & Gurr 1998; Siekmann *et al.* 2001; Wäckers 2001; Costamagna & Landis 2004; Lee *et al.* 2004). Presence of nectar and pollen may have a marked effect on the effectiveness of natural enemies controlling pest insect populations (Tylianakis *et al.* 2004). Chrysopids, coccinellids, syrphids and parasitoids have been shown to use extra-field nectar sources and spread into surrounding crops (Hickman & Wratten 1996; Freeman Long *et al.* 1998; Nicholls *et al.* 2001) where they may suppress pest populations (White *et al.* 1995; Tylianakis *et al.* 2004). However, insects are selective in their use of flowering plant species (Patt *et al.* 1997; Wäckers 2004) and specific plants may provide food for either pest species or natural enemies (Baggen *et al.* 1999; Wäckers 2001). The composition of the flora is therefore an important factor for the potential pest suppressive effect of non-crop habitats.

Wooded habitats also provide a more moderate microclimate than field centres (Forman & Baudry 1984). This is of particular importance for parasitoids that may experience considerably shorter lifespans at high temperatures (Rahim *et al.* 1991; Hailemichael & Smith 1994). The moderate microclimate in combination with presence of nectar sources in wooded edges result in higher parasitoid longevity, early season abundance (Dyer & Landis 1996, 1997) and higher levels of parasitism as compared to field centres (Landis & Haas 1992).

Natural enemies and pest species also use non-crop habitats for hibernation. *Rosa* species, spindle tree (*Euonymus* spp.) and bird cherry (*Prunus padus* (L.)), which are typically found in woody habitats, function as winter host of the pest aphids *Metopolophium dirhodum* (Walker), *Aphis fabae* (L.) and *Rhopalosiphum padi* (L.), respectively (Leather 1993). Coccinelids (e.g. Zhou *et al.* 1995), carabid beetles, staphylinids (e.g. Sotherton 1985), parasitoids (Corbett & Rosenheim 1996) and spiders (Jmhasly & Nentwig 1995) also hibernate in woody and herbaceous habitats. In particular, raised earth banks containing tussock-forming vegetation—so-called beetle banks—provide favourable conditions for hibernation and are associated with high densities of hibernating predators (Thomas *et al.* 1991). Natural enemies that hibernate in non-crop habitats have been shown to invade surrounding fields (Honěk 1982; Coombes & Sotherton 1986; Thomas *et al.* 1991; Dennis & Fry 1992; Corbett & Rosenheim 1996), where they may limit the population increase of pests (Landis & van der Werf 1997; Menalled *et al.* 1999*a*; Collins *et al.* 2002).

We conclude that non-crop habitats provide important life-support functions that are essential for a wide range of natural enemies. Non-crop habitats can therefore enhance the abundance and diversity of natural enemy species in the agricultural landscape. However, depending on their vegetation composition, non-crop habitats can also stimulate potential pest species.

4. LANDSCAPE MEASURES AFFECTING NATURAL PEST CONTROL

Natural enemy species differ in their dispersal ability, which impacts their response to the spatial distribution of non-crop habitats in the landscape (Tscharntke *et al.* 2005). Mobile species may respond to the proportion of non-crop habitat at the landscape scale. For instance, abundances of ballooning spiders respond at a scale of several kilometres (Schmidt & Tscharntke 2005*a*) and parasitoids at a scale ranging from two kilometres to a couple of hundreds of metres (Kruess & Tscharntke 1994; Thies *et al.* 2005). The differential habitat use and dispersal ability of natural enemies are likely to affect species composition, species interactions and pest control at the landscape level.

The spatial distribution of crop and non-crop habitats may also affect natural pest control at the field scale as many generalist predators colonize crops from adjoining non-crop hibernation quarters early in the season (Coombes & Sotherton 1986; Thomas *et al.* 1991; Dennis & Fry 1992; Corbett & Rosenheim 1996; Petersen 1999). Small-scale landscapes that are rich in non-crop habitats have extended crop and non-crop interfaces and allow an effective early season field colonization by natural enemies (Bianchi & van der Werf 2003). The timely arrival of natural enemies in crops is considered an important prerequisite for successful pest control because pest populations have little time for unrestricted increase (Settle *et al.* 1996; Landis & van der Werf 1997). In addition, many nectar-feeding natural enemies such as parasitoids, syrphids and chrysopids are more abundant near field edges than in field centres (Landis & Haas 1992; Baggen & Gurr 1998; Freeman Long *et al.* 1998; Thies & Tscharntke 1999; Nicholls *et al.* 2001; Tylianakis *et al.*

2004). In small-scale landscapes with extended crop and non-crop boundaries, a relatively large proportion of the crop area is therefore likely to be subject to increased activity of natural enemies.

There are indications that parasitoids and predators may generally act at smaller spatial scales than herbivores and are therefore more susceptible to habitat fragmentation (Zabel & Tscharntke 1998; Kruess & Tscharntke 2000; Cronin 2004). For instance, the abundance and diversity of parasitoid communities have been shown to decrease with increasing distance from non-crop habitats, resulting in reduced parasitism (Kruess & Tscharntke 1994, 2000; Tscharntke *et al.* 1998). As habitat connectivity is likely to be lower in simplified, large-scale landscapes than in complex, small-scale landscapes, large-scale landscapes may only support an impoverished parasitoid community and have an increased risk of pest outbreaks when herbivores are released from natural enemy control.

In conclusion, spatial scale and the distribution of crop and non-crop habitats in the landscape may influence the natural pest control function via multiple mechanisms. The diversity and density of natural enemy populations may decline with increasing distance from non-crop habitats, and the average distance between non-crop habitats and fields may affect the timing of field colonization. Diversified small-scale landscapes therefore provide better conditions for effective pest control by natural enemies than do large-scale landscapes.

5. EFFECTS OF LANDSCAPE COMPOSITION ON NATURAL ENEMIES AND PEST PRESSURE

We have shown from our review of the literature that non-crop habitats act as reservoirs for biodiversity in agricultural landscapes and provide requisites for natural enemies that have the potential to control insect pests. In addition, we hypothesized that complex landscapes have a more favourable arrangement of crop and non-crop habitats for pest regulation than simple landscapes. Often, landscape patchiness and the proportion of non-crop habitats are positively correlated, at least because field borders often contain semi-natural vegetation (Basedow 1990; Ryszkowski & Karg 1991; Menalled *et al.* 1999*b*). We hypothesize that pest control is positively related to the proportion of non-crop habitat in the surrounding landscape and to landscape patchiness. To test this hypothesis we collected articles in scientific journals that quantified pest pressure and activity of natural enemies in crops in relation to landscape composition. Landscapes with high proportions of forest, hedgerows, tree lines, field margins, grassland, fallows, channels or wetlands are referred to as 'complex', landscapes with few of these habitats as 'simple'. Small-scale and large-scale landscapes, as indicated by perimeter-to-area ratios of fields or landscape patchiness, were also classified as complex and simple, respectively. Articles were retrieved from literature databases (Current Contents and Biological Abstracts; see http://www.isinet.com/) and relevant articles from 'grey' literature were included as well. Criteria for article selection were: (i) studies should be conducted at the landscape scale; (ii) studies should explicitly incorporate effects of non-crop habitats on pest regulation in crops; (iii) the experimental set-up should allow a proper statistical analysis; and (iv) there should be no obvious confounding effects of environmental factors, such as soil fertility (see Smeding & Booij 1999; Freier *et al.* 2003). Twenty eight studies matched our criteria (table 1), whereas seven relevant studies were not included because the criteria were not fully met (Ryszkowski & Karg 1991; Ryszkowski *et al.* 1993; Kruess & Tscharntke 1994; Jonsen & Fahrig 1997; Smeding & Booij 1999; Freier *et al.* 2003; van Alebeek *et al.* 2003). We recorded the number of cases where landscape complexity had a positive, neutral or negative effect on natural enemies and pest pressure and recorded the magnitude of the effects. Because many studies reported dissimilar results for different years, landscape pairs, natural enemy species or non-crop habitat types, the information was split up for the respective years, landscape pairs etc., and referred to as observations. The 28 studies were classified according to the proportions of observations having a positive, neutral or negative effect. For instance, Menalled *et al.* (1999*b*) found a positive effect of landscape complexity on parasitism rate in one landscape pair and no effect in two other landscape pairs. This study was therefore counted as one-third positive and two-thirds neutral. Observations were considered positive or negative when significant at the 95% confidence level.

Enhancement of natural enemy populations in crop fields was quantified in 24 studies (table 2) and was expressed in (activity) density (studies no. 1, 6, 7, 8, 9, 18, 19, 20, 24, 25), parasitism rate (studies no. 2, 4, 13, 14, 15, 21, 22, 23, 26, 27, 28), fecundity (study no. 3), oviposition rate (study no. 12), predation rate (study no. 2) and condition of natural enemies (study no. 17). Complex landscapes resulted in enhanced natural enemy populations in 74.0% of the studies and included a variety of arthropod natural enemies and all types of enhancement effects. The sizes of enhancement effects ranged from 1.6 times higher oviposition rates of syrphids (Krause & Poehling 1996) to 10 times higher parasitism rates in complex versus simple landscapes (Thies *et al.* 2003). Landscape composition did not affect natural enemy populations in 20.8% of the studies. In these cases the oviposition rates of syrphids (Krause & Poehling 1996), parasitism rates in armyworms (Menalled *et al.* 1999*b*, 2003; Costamagna *et al.* 2004), activity density of carabid beetles (Purtauf *et al.* 2005*a*,*b*) and spider densities (Schmidt & Tscharntke 2005*a*) did not respond to landscape composition. In 5.1% of the studies, the activity of natural enemy was lower in complex landscapes than in simplified landscapes. These observations concern densities of a damsel bug and four coccinellid species that were negatively correlated to patch diversity, wetlands, set-aside land (USDA Conservation Restoration Program), forest, landscape patchiness or pasture (Elliott *et al.* 2002*a*,*b*) and 20% reduced parasitism rates in armyworm larvae in complex versus simple landscapes (Menalled *et al.* 2003).

Pest pressure was quantified in 10 studies (table 3). Pest pressure was expressed in densities (studies no. 1, 5, 9, 10, 11, 16, 21, 28), crop injury levels (studies no. 5, 26, 27) and aphid establishment, survival or population growth rate (study no. 16). In 45.0% of the studies, pest pressure was reduced in complex landscapes. Effects included (strong) reductions of aphid densities (Basedow 1990; Östman *et al.* 2001*a*), thrips densities and thrips

Table 1. Summary of selected articles that quantified pest pressure and natural enemy stimulation in crops in relation to landscape composition.

no.	authors	landscape factors	crop	pest species group	natural enemy species group
1	Basedow (1990)	field margins, hedges, field size	sugar beet	aphids	aphid predator complex
2	Bianchi *et al.* (2005)	forest, tree lines, grassland, channels	brussels sprout	—	predators, egg parasitoids
3	Bommarco (1998)	field area-to-perimeter ratio	cereals, rapeseed, legumes	—	carabid beetles
4	Costamagna *et al.* (2004)	wooded field edges, field size	maize	—	armyworm parasitoids
5	Den Belder *et al.* (2002)	forest	leek	thrips	—
6	Elliott *et al.* (1998)	forest, grassland, CRP[a], patchiness	wheat	—	aphid predator complex
7	Elliott *et al.* (2002*a*)	forest, CRP, grassland, wetlands, patchiness	maize	—	coccinellids
8	Elliott *et al.* (2002*b*)	forest, CRP, wetlands, patchiness	alfalfa	—	aphid predator complex
9	Galecka (1966)	forest	potato	aphids	coccinellids
10	Holland & Fahrig (2000)	wooded field edges	alfalfa	weevils	—
11	Klug *et al.* (2003)	forest	spinach	Lepidoptera	—
12	Krause & Poehling (1996)	hedges	winter cereals	—	syrphids
13	Marino & Landis (1996)	wooded field edges, field size	maize	—	armyworm parasitoids
14	Menalled *et al.* (1999*b*)	wooded field edges, field size	maize	—	armyworm parasitoids
15	Menalled *et al.* (2003)[b]	wooded field edges, field size	maize	—	armyworm parasitoids
16	Östman *et al.* (2001*a*)	field area-to-perimeter ratio, forest	spring barley	aphids	—
17	Östman *et al.* (2001*b*)	field area-to-perimeter ratio	cereal	—	carabid beetles
18	Prasifka *et al.* (2004)	uncultivated areas	cotton	—	cotton natural enemy complex
19	Purtauf *et al.* (2005*a*)	forest, fallow, hedgerows, grassland	winter wheat	—	carabid beetles
20	Purtauf *et al.* (2005*b*)	forest, fallow, hedgerows, grassland	winter wheat	—	carabid beetles
21	Roschewitz *et al.* (2005)	forest, fallow, hedgerows, grassland	winter wheat	aphids	aphid parasitoids
22	Sedivý (1995)	ecological corridors	wheat	—	leaf beetle parasitoids
23	Schmidt *et al.* (2003)	forest, fallow, hedgerows, grassland	winter wheat	—	aphid parasitoids
24	Schmidt & Tscharntke (2005*a*)	forest, fallow, hedgerows, grassland	winter wheat	—	spiders
25	Schmidt *et al.* (2005)	forest, fallow, hedgerows, grassland	winter wheat	—	spiders
26	Thies & Tscharntke (1999)	forest, fallow, hedgerows, grassland	oilseed rape	rape pollen beetle	rape pollen beetle parasitoids
27	Thies *et al.* (2003)	forest, fallow, hedgerows, grassland	oilseed rape	rape pollen beetle	rape pollen beetle parasitoids
28	Thies *et al.* (2005)	forest, fallow, hedgerows, grassland	winter wheat	aphids	aphid parasitoids

[a] Conservation Reserve Program: unmanaged grassland.
[b] Landscape pairs already incorporated in Marino & Landis (1996) and Menalled *et al.* (1999*b*) were discarded to avoid double counts.

symptoms in leek (Den Belder *et al.* 2002) and reductions in crop injury by rape pollen beetles in oilseed rape (Thies & Tscharntke 1999; Thies *et al.* 2003). Landscape composition did not affect pest pressure in 40.0% of the studies. Galecka (1966) and Thies *et al.* (2005) found in complex landscapes both higher aphid establishment rates and aphid mortality rates inflicted by natural enemies in potato and cereal, resulting in a similar aphid pressure in complex and simplified landscapes. Klug *et al.* (2003) found no effect of forests on the density of *Autographa gamma* (L.) larvae, and Holland & Fahrig (2000) reported that densities of weevils infesting alfalfa fields were not

Table 2. Overview of the effect of landscape complexity on natural enemies (results of an analysis including 24 studies). (Score indicates the fraction of observations that have a significant positive, negative or non-significant effect (95% confidence level); effect size indicates the ratio between the natural enemy impact in complex versus simple landscapes; and type denotes the response variable (d; (activity) density, p; parasitism, f; fecundity, o; oviposition, pr; predation rate, c; condition).)

increased				neutral				decreased			
reference	score	effect size	type	reference	score	effect size	type	reference	score	effect size	type
Basedow (1990)	1	2.4, 2.9	d	Costamagna *et al.* (2004)	1	1.2	p	Elliott *et al.* (2002*a*)	0.5	n.d.	d
Bianchi *et al.* (2005)	1	n.d.	pr, p	Krause & Poehling (1996)	0.33	0.7	—	Elliott *et al.* (2002*b*)	0.4	n.d.	d
Bommarco (1998)	1	2.5	f	Menalled *et al.* (1999*b*)	0.67	0.4, 1.2	p	Menalled *et al.* (2003)	0.33	0.8	p
Elliott *et al.* (1998)	1	n.d.	d	Menalled *et al.* (2003)	0.67	0.7, 0.9	p	—	—	—	—
Elliott *et al.* (2002*a*)	0.5	n.d.	d	Purtauf *et al.* (2005*a*)	1	n.d.	d	—	—	—	—
Elliott *et al.* (2002*b*)	0.6	n.d.	d	Purtauf *et al.* (2005*b*)	1	2.5	d	—	—	—	—
Galecka (1966)	1	2.4	d	Schmidt & Tscharntke (2005*a*)	0.33	n.d.	d	—	—	—	—
Krause & Poehling (1996)	0.67	1.6, 4.3	o	—	—	—	—	—	—	—	—
Marino & Landis (1996)	1	5.5	p	—	—	—	—	—	—	—	—
Menalled *et al.* (1999*b*)	0.33	8	p	—	—	—	—	—	—	—	—
Östman *et al.* (2001*b*)	1	n.d.	c	—	—	—	—	—	—	—	—
Prasifka *et al.* (2004)	1	n.d.	d	—	—	—	—	—	—	—	—
Roschewitz *et al.* (2005)	1	2	p	—	—	—	—	—	—	—	—
Sedivý (1995)	1	2.4	p	—	—	—	—	—	—	—	—
Schmidt *et al.* (2003)	1	2	p	—	—	—	—	—	—	—	—
Schmidt & Tscharntke (2005*a*)	0.67	2.1, 5	d	—	—	—	—	—	—	—	—
Schmidt *et al.* (2005)	1	n.d.	d	—	—	—	—	—	—	—	—
Thies & Tscharntke (1999)	1	2.5	p	—	—	—	—	—	—	—	—
Thies *et al.* (2003)	1	10	p	—	—	—	—	—	—	—	—
Thies *et al.* (2005)	1	2.6, 4, 7	p	—	—	—	—	—	—	—	—
total score	17.77				5.00				1.23		
percentage	74.0%				20.8%				5.1%		

affected by the presence of woody field borders. In 15% of the studies, increased pest pressure was found with increasing landscape complexity. Roschewitz *et al.* (2005) found higher densities of wheat aphids in complex landscapes as compared to simple landscapes because of increased aphid establishment. Östman *et al.* (2001*a*) found a negative relationship between the impact of natural enemies on the aphid population growth rate and the proportion of forest at a scale of 400×400 m. These findings suggest that under certain conditions and for certain sets of species non-crop habitats in the direct vicinity of crops may attract generalist predators, leading to reduced pest control in arable fields.

The analysis highlighted differential responses of aphids in cereal crops to landscape composition (Östman *et al.* 2001*a*; Roschewitz *et al.* 2005; Thies *et al.* 2005). The study of Östman *et al.* (2001*a*) focused on *R. padi*, which uses *P. padus* as winter host, whereas in the studies of Roschewitz *et al.* (2005) and Thies *et al.* (2005) *Sitobion avenae* was the dominant aphid species, which hibernates on perennial grasses. In the study of Östman *et al.* (2001*a*) in which lower aphid pressure was found in complex landscapes than in simple landscapes, there was no indication that *R. padi* colonized cereal crops from non-crop habitats. In this case, non-crop habitats may have favoured natural enemies only and not *R. padi*. In the

Table 3. Overview of the effect of landscape complexity on pest pressure (results of an analysis including 10 studies). (Score indicates the fraction of observations that have a significant positive, negative or non-significant effect (95% confidence level); effect size indicates the ratio between the pest pressure in complex versus simple landscapes; and type denotes the response variable (d; density, c; crop injury, e; establishment and survival, r; population growth rate).)

reduced				neutral				increased			
reference	score	effect size	type	reference	score	effect size	type	reference	score	effect size	type
Basedow (1990)	1	0.05, 0.07	d	Galecka (1966)	1	n.d.	d	Östman *et al.* (2001*a*)	0.5	n.d.	r
Den Belder *et al.* (2002)	1	n.d.	d	Holland & Fahrig (2000)	1	n.d.	d	Roschewitz *et al.* (2005)	1	1.4	d
Östman *et al.* (2001*a*)	0.5	0.6	e	Klug *et al.* (2003)	1	n.d.	d	—	—	—	—
Thies & Tscharntke (1999)	1	0.6	c	Thies *et al.* (2005)	1	n.d.	d	—	—	—	—
Thies *et al.* (2003)	1	0.6	c	—	—	—	—	—	—	—	—
total	4.5				4				1.5		
percentage	45.0%				40.0%				15.0%		

studies of Roschewitz *et al.* (2005) and Thies *et al.* (2005), who found negative and neutral effects of non-crop habitat on aphid populations, there were clear indications that the presence of alternative host plants in non-crop habitats boosted *S. avenae* populations. In this case, non-crop habitats favoured both natural enemies and pests. Thus, the interaction between pest species and non-crop vegetation is a key factor that can alter the outcome of landscape effects on natural pest control.

6. IDENTIFICATION OF LANDSCAPE FACTORS AFFECTING NATURAL PEST CONTROL

The coarse-scale analysis revealed that the proportion of non-crop habitats and patchiness of the landscape may affect natural enemy populations and pest pressure in crops. However, non-crop habitats comprise many vegetation types, each affecting natural enemies and pests potentially in a different way. In a second, fine-scaled analysis we assess in more detail what type of landscape factors are associated with natural pest regulation. Simple and complex landscapes differed in most cases in landscape patchiness and the proportions of woody and herbaceous habitats. We recorded how often these landscape factors were related using observations of positive, neutral or negative effects on natural enemies and pest pressure (tables 2 and 3). We distinguished between studies that identified effects of a single factor (e.g. forest; Den Belder *et al.* 2002) and studies that revealed the combined effect(s) of multiple factors (e.g. wooded field edges and field size; Marino & Landis 1996). Studies that incorporated multiple landscape factors were proportionally classified over each factor. Hence, wooded habitats and landscape patchiness each counted as half for Marino & Landis (1996), whereas wooded habitats counted as one for Den Belder *et al.* (2002).

Landscapes with enhanced natural enemy populations contained in most cases herbaceous habitats or wooded habitats and less frequently a patchy landscape composition (table 4). When expressed in percentages in each category, enhanced activity of natural enemies was most frequently associated with herbaceous habitats (80%) and somewhat less often with wooded habitats (71%) and landscape patchiness (70%). There were only relatively few observations of landscape composition affecting pest pressure. Reduced pest pressure was most often associated with landscape patchiness and less often with herbaceous habitats and wooded habitats. However, the few observations on pest density in crops do not allow a general conclusion regarding effects of landscape factors on pest pressure.

Table 4. Frequency of three landscape factors present in landscapes with increased '+', neutral '0' and reduced '−' activity of natural enemies and pest pressure.

	effect	wooded habitats	herbaceous	landscape patchiness
natural enemies	+	6.45 (71%)	7.31 (80%)	3.61 (70%)
	0	2.28 (25%)	1.55 (16%)	1.17 (23%)
	−	0.37 (4%)	0.40 (4%)	0.37 (7%)
pest pressure	−	2.00 (32%)	1.67 (56%)	0.83 (100%)
	0	3.33 (54%)	0.67 (22%)	0 (0%)
	+	0.83 (14%)	0.67 (22%)	0 (0%)

7. DISCUSSION

(a) *How robust are landscape effects on natural pest control?*

In this review, we have documented effects of landscape composition on natural enemies in 24 studies and showed that landscape complexity enhanced natural enemy populations in 74% of the cases. Natural enemy groups studied were parasitoids, carabid beetles, coccinellids, syrphid larvae, damsel bugs, chrysopids, staphylinids and spiders. Positive effects were reported for each of these groups. Landscape-driven stimulation of natural enemy populations can therefore be considered a general phenomenon. Enhanced populations of natural enemies in crops, however, provide no guarantee for effective pest control. From an agronomic point of view, effects of landscape composition on pest densities are much more relevant than effects on natural enemies. Yet we only found 10 such studies, in which landscape complexity resulted in suppressed pest populations in 45% of the cases. We conclude that landscape complexity may stimulate pest suppression in particular cases, but the low number of studies that met the criteria for our analysis prohibits drawing general conclusions on this issue. The limited data suggest that landscape effects may be specific for herbivore species. For instance, densities of rape pollen beetles were in all cases negatively correlated to landscape complexity (Thies & Tscharntke 1999; Thies *et al.* 2003), whereas aphid densities showed a variable response to landscape complexity (e.g. Basedow 1990; Roschewitz *et al.* 2005; Thies *et al.* 2005). Furthermore, there was a tendency for pest pressure to be positively correlated with cropping area (Jonsen & Fahrig 1997; Den Belder *et al.* 2002; Klug *et al.* 2003; but see Roschewitz *et al.* 2005), suggesting that the prime sources of most pest species are arable fields and that non-crop habitats may act as sources of pests only for specific vegetation-pest species combinations.

Circumstantial evidence provided by studies that were discarded for our analysis because of the lack of a proper statistical analysis indicates that positive effects of landscape complexity on pest suppression may be common in a wider range of systems. Ryszkowski & Karg (1991) and Ryszkowski *et al.* (1993) reported higher biomass of pest species in crops located in simple versus complex landscapes in Romania and Poland. van Alebeek (2003) reported two- and threefold lower aphid densities in wheat and potato, respectively, in a 10 ha organic cropping system containing a network of permanent field margins as compared to a control area without such a network. In Germany, landscape mosaics composed of forests, arable crops and networks of hedgerows provide long-term natural pest control, as aphid densities are kept below economic thresholds by an abundant and diverse natural enemy complex. These are some of the few regions in Germany where there is no need for chemical aphid control (Ohnesorge & Schier 1989; references cited in Schulze & Gerstberger 1993). When this circumstantial evidence is taken into account, landscape-driven pest control in 45% of the cases may be considered as a conservative estimate.

(b) *Future directions*

There is a clear need for more studies that investigate effects of landscape composition on interactions between communities of natural enemies and herbivores, and crop production. Future research should ideally quantify all of the following aspects in an integrated way: (i) the stimulation of natural enemy populations; (ii) colonization of arable fields by natural enemies; (iii) reducing pest densities; (iv) reducing damage levels; (v) increasing yield; and (vi) improving cost–benefit. Thus far, most studies have focused on the first step but concentrated mainly on parasitoids, carabid beetles and coccinellids, and there is no or only scarce information on other important natural enemy groups, such as larvae of chrysopids and gall midges, predatory bugs, staphylinids or insectivorous birds. A limited number of studies have quantified the colonization of fields (step ii), mainly for ground-dwelling predators and parasitoids, and few studies have quantified landscape-scale effects on reducing pest densities (step iii). We know of three studies that have related crop injury to landscape composition (Thies & Tscharntke 1999; Den Belder *et al.* 2002; Thies *et al.* 2003). Effects of landscape composition on yield increment (step v) and improving cost–benefit (step vi) have rarely been quantified (Östman *et al.* 2003). Hence, here lies a clear knowledge gap which must be filled before we can assess the pest control function of landscapes in monetary terms.

Another unresolved issue is the definition of the mechanisms by which landscape composition drives natural enemy–herbivore interactions. The contrasting parasitism patterns in different complex–simple landscape pairs (Menalled *et al.* 1999*b*) and landscape-specific year-to-year variation in parasitism rates (Menalled *et al.* 2003) are as yet unexplained. Landscape complexity is generally associated with small fields, which allow effective colonization by natural enemies, high densities of natural enemies and high diversity of the natural enemy complex. Positive effects of landscape complexity on natural pest control may therefore be attributed to a joint effect of these factors, which are often strongly correlated and difficult to unravel. Early season colonization may prevent the rapid build-up of pest populations and high densities of natural enemies may suppress pest populations in crops by increased removal of pest numbers, whereas the diversity of natural enemies may increase ecosystem stability because rich communities have an increased likelihood of containing species that are well adapted to various conditions (Yachi & Loreau 1999; Ives *et al.* 2000). So far, the contribution of each of these mechanisms to pest control has received little or no attention. Identification of the key factors that drive natural pest control at the landscape scale may provide insight into the unexplained variation in natural enemy and herbivore densities in time and space.

Biodiversity restoration programs, such as agri-environment schemes, may offer an opportunity to restore the pest control function in rural landscapes. To date, there is only little knowledge of how this should be done. Questions like 'In what landscapes is such habitat management expected to be most effective?' and 'What vegetation types and spatial arrangement of non-crop habitat are likely to enhance natural pest control?' have received only very limited attention. The sigmoid-shaped relationship between the proportion of non-crop habitat and crop injury suggests that the effectiveness of habitat management is not likely to be the same in all landscapes (Thies & Tscharntke 1999). The benefit per area unit of added non-crop habitat might be the highest in landscapes that have proportions of non-crop habitat near the inflection point of the sigmoid curve. Indeed, there is evidence of a threshold value of 20% non-crop area above which differences in parasitism levels in field edges and field centres disappeared and pest control was observed throughout the fields (Tscharntke *et al.* 2002). The fine-scale analysis suggests that a variety of non-crop habitats may enhance the pest control function of ecosystems because herbaceous and wooded habitats were, in 80 and 71% of the cases, associated with enhanced natural enemy populations. A modelling study further suggests that the spatial arrangement and shape of non-crop habitats may affect pest suppression profoundly (Bianchi & van der Werf 2003). These hypotheses may be tested by studying dynamics of natural enemies and herbivores in different landscape types in response to establishment of new non-crop habitats. Such an experimental landscape approach may provide crucial information for the development of future habitat management strategies that restore the pest control function in agroecosystems.

(c) *Synthesis*

This review highlights the importance of non-crop habitats for the conservation of a wide range of biota in agricultural landscapes, including many natural enemy species. Complex landscapes comprising dense networks of non-crop habitats provide favourable conditions and requisites for natural enemy populations, often resulting in increased natural enemy activity in crop fields. Landscape complexity may also give rise to suppressed pest populations, but these effects are difficult to generalize as only relatively few studies have addressed this issue. There is a need for more studies that quantify effects of landscape composition on the cascading effects of natural enemies, herbivore populations, and crop production and express the benefit of the pest control function in monetary terms. The significance of the spatial context for the pest control function implies that incentives for implementing functional biodiversity in cropping systems should not only focus on local management practices, but also incorporate management at the landscape scale. Multiple non-crop habitat types may favour natural pest control as grassland, herbaceous and wooded habitats all were associated with enhanced natural enemy populations. Since different non-crop habitat types may support distinct plant, herbivore and natural enemy communities, diversified landscapes may hold the most potential for the conservation of biodiversity and sustaining the pest control function.

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